

Current Biology

Early Permian synapsid impressions illuminate the origin of epidermal scales and aggregation behavior

Highlights

- *Bromackerichnus* n. igen. is the earliest resting trace of synapsids
- *Bromackerichnus* includes the earliest epidermal scales of synapsids
- Eight tetrapod groups had epidermal scales during the early Permian global warming
- *Bromackerichnus* associations suggest group behavior of sphenacodonts

Authors

Lorenzo Marchetti, Antoine Logghe, Michael Buchwitz, Jörg Fröbisch

Correspondence

lorenzo.marchetti@mfh.berlin

In brief

Marchetti et al. describe *Bromackerichnus*, the first definite body impression of early synapsids and, more specifically, sphenacodontids. *Bromackerichnus* includes the earliest fossil evidence of epidermal scales in synapsids, long before the acquisition of hair. Marchetti et al. evidence how the acquisition of epidermal scales might be related to the early Permian aridization. *Bromackerichnus* is a resting trace found in associations co-occurring with swimming and sliding traces, evidencing gathering of sphenacodonts in or near pools.



Report

Early Permian synapsid impressions illuminate the origin of epidermal scales and aggregation behavior

Lorenzo Marchetti,^{1,5,*} Antoine Logghe,² Michael Buchwitz,³ and Jörg Fröbisch^{1,4}¹Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany²Centre de Recherche en Paléontologie – Paris, UMR 7207 – CNRS, MNHN, SU, Muséum National d'Histoire Naturelle, 8 rue Buffon, CP38, Paris, France³Museum für Naturkunde Magdeburg, Otto-von-Guericke-Straße 68-73, 39104 Magdeburg, Germany⁴Institut für Biologie, Humboldt-Universität zu Berlin, Invalidenstraße 42, 10115 Berlin, Germany⁵Lead contact*Correspondence: lorenzo.marchetti@mfn.berlin<https://doi.org/10.1016/j.cub.2025.04.077>

SUMMARY

Fossil evidence of skin structure^{1,2} and group behavior^{3,4} in the stem group of mammals, the early synapsids, is sparse and restricted to a few occurrences. We describe here exceptional resting trace fossils, *Bromackerichnus requiescens* n. igen. n. isp., from the early Permian Tambach Formation at the Bromacker locality, Thuringia, Germany.⁵ They are the only definite early synapsid—and, more specifically, spenacodontid—full-body impressions. They include skin impressions of the limbs, trunk, and tail that show epidermal scales and are associated with *Dimetropus leisnerianus* footprints. Through a morphological comparison with modern taxa,⁶ we demonstrate for the first time the unequivocal occurrence of epidermal scales in early synapsids. A review of the early amniote and stem amniote trace and body fossil skin record highlights that this constitutes the oldest occurrence of epidermal scales in synapsids, long before the acquisition of hair.⁷ Moreover, we find the first fossil occurrence of epidermal scales in eight different tetrapod groups during the early Permian. This implies an earlier common origin of epidermal scales. The higher chance of preservation and spreading in the early Permian was probably due to a structural reinforcement of the scales as an adaptation to global warming and aridization⁸ at the end of the Late Paleozoic Ice Age. Moreover, spenacodontid resting, swimming, and locomotion traces of multiple individuals of different sizes co-occur on the same bedding planes, in a relatively small area. This is interpreted as the earliest documented aggregation behavior in spenacodontid synapsids that gathered in and around small ponds.

RESULTS

Systematic paleontology

Bromackerichnus requiescens n. igen. n. isp. Figures 1 and 2 and Table S1.

Etymology

From the Bromacker locality, Latin *ichnus*, trace, and Latin *requiescens*, resting.

Material

Holotype MNG 1821 (holotype), MNG 1765 and MNG 14944 (paratypes), MNG 1822, MNG 1828, MNG 1983, MNG 1987, and MNG 13490. Fine-grained sandstones with traces preserved as natural casts.

Type locality

Bromacker locality, Thuringia, Germany. Tambach Sandstone Member, Tambach Formation (Cisuralian, Sakmarian), Thuringian Forest Basin (Figure S1).

Diagnosis

Resting trace of a tetrapod (with a trunk about 8–16 cm wide). The trunk impression is craniocaudally short and transversally broad compared with the putative neotridian resting trace *Hermundurichnus*,⁹ which is instead characterized by a thin trunk impression. No medial ridges or lines are observed, different from *Temnocorpichnus*¹⁰ and *Hermundurichnus*. Semi-lunate lateral skin flap impressions as those observed in *Hermundurichnus* are not present. The forelimb impressions are at a low angle compared with the trunk impression, different from *Temnocorpichnus*, in which the forelimbs are perpendicular to the trunk impression. Limb impressions are relatively smaller, compared with the body, than in *Temnocorpichnus*. The relatively thin (about 1/6 of the trunk width) and straight tail impression differs from *Temnocorpichnus*, which shows a wider (about 1/3 of the trunk width) and shorter tail impression. The occurrence of scale impressions on trunk, limbs, and tail differs from *Temnocorpichnus*, which does not show scaly skin impression. The rhomboidal to rectangular scale impressions of the trunk are aligned in a grid of slightly caudolaterally bent transversal and longitudinal rows

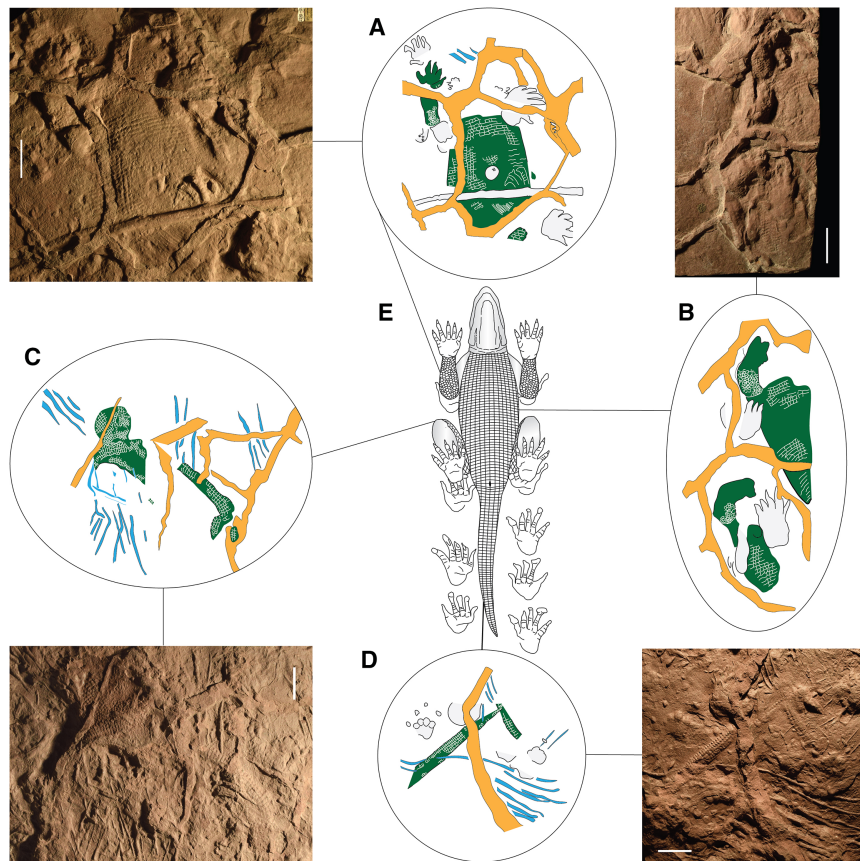


Figure 1. Spnenadontid body impression, *Bromackerichnus requiescens* n. igen. n. isp.

(A–D) Photos with oblique light and interpretive drawings. All specimens in convex hyporelief; scale bars, 5 cm. Body impressions in green, swimming traces in blue, footprints and other trace fossils in gray, and mud cracks in orange. (A) MNG 1821, holotype. Trunk and right forelimb impressions with scalation pattern, right manus and left pes impressions (*Dimetropus leisnerianus*) with scale grooves. (B) MNG 1765, paratype. Two body impressions side by side, showing trunk impressions and right forelimbs with scalation pattern and indistinct manus impressions. (C) and (D) MNG 14944, paratype. (C) Two body impressions. The one on the left of the photo includes lower trunk, pelvic and proximal tail, and right hindlimb impressions with scalation pattern. The one on the right of the photo includes tail and left proximal hindlimb impressions with scalation pattern. (D) Two tail impressions with scalation pattern, crossing each other at right angle.

(E) Reconstruction of the producer of *Bromackerichnus requiescens* n. igen. n. isp. with scalation pattern and hypothetical trackway leading to the resting position, bottom view. The gray areas are not impressed. Artwork by Sophie König.

that differ from *Hermundurichnus*, in which these scale impressions are aligned in rows with a more irregular pattern. The forelimb ends in a pentadactyl manus impression and the body trace is associated with a pes impression, which are both assignable to *Dimetropus leisnerianus*, different from *Temnocorpichnus*, in which the forelimb ends in a tetradactyl manus impression assignable to *Batrachichnus salamandroides*.

Description

Body impression of a tetrapod with a relatively short (16–24 cm) and wide (8–16 cm) trunk (Figures 1A and 1B). The whole trunk impression is characterized by rhomboidal to rectangular scales, each about 4 or 5 mm long and wide, arranged in a grid of transversal and longitudinal (craniocaudal) rows. The transversal rows are slightly bent caudolaterally. Scales on the lateral parts of the trunk are slightly more prominent; this is observable in the scale profiles (Figures 2E and 2G; sections 4 and 5). No medial ridges are observed. No head and neck impressions are preserved. Forelimb impressions are relatively short and thick compared with the body (Figures 1A and 1B), with the orientation of the lower arms diverging at a low angle from the trunk (-19° to 11°). Forelimb width is 3 cm, length 5–6 cm. The distal forelimb impression is covered by oblique-trending rows of hexagonal scale impressions, each about 2 or 3 mm in diameter, which sometimes follow a regular arrangement. These scales are smaller and more prominent than those on the trunk. They show a profile with higher relief (Figure 2D; sections 2 and 3). Only the proximal part of the hindlimb

impression is preserved and is about 6 cm wide, at a relatively high angle to the trunk (44° – 57° , Figure 1C). The proximal hindlimb impression is covered by rectangular (limb side facing the tail) to hexagonal scales (ventral side of the limb) about 5 mm long and wide, perpendicular to the limb direction. These rows are slightly curved, following the curvature of the limb, and show scales overlapping on the ventral side of the limb. These scales show an asymmetric profile, having sides of different lengths and inclinations (Figure 2I; section 7). The connection between tail and hindlimb is distinctly curved, and the side shows regular rows of rectangular scales. Tail impressions are straight, long, and thin (Figures 1C and 1D). The maximum tail length is about 26 cm, and tail width is about 3 cm. The tail impression is covered by longitudinal rows of rectangular and prominent scales. These scales show a profile with high relief and clear hinge regions (Figure 2K; sections 8 and 9).

Associated traces

The right forelimb of the resting trace of MNG 1821 ends in a pentadactyl, ectaxonic (i.e., with relatively longer lateral digits) manus impression about 5 cm long and 6 cm wide (Figure 1A). Digit IV is the longest, digit V is about as long as digit II (Table S1). Digit imprints end in sharp claw impressions and show rectangular scales as wide as the digits, about 5 mm in length. An associated incomplete left pes imprint is 5 cm long and 6 cm wide (Figure 1A). It is ectaxonic; digit IV is the longest, digit V is shorter than digit II (Table S1). Digit II ends in a bifurcated impression. Digits show clear rectangular scales as wide as the digits and about 5 mm in length. Complete autopodia impressions, ectaxonic,



Figure 2. Scale impressions of spheonacodontids

Body impressions of *Bromackerichnus requiescens* n. igen. n. isp. associated with *Dimetropus leisnerianus* footprints.

(A and B) MNG 1983. (A) Incomplete step cycle with left pes-manus couple and left pes associated with a tail impression with rectangular scalation pattern. (B) Left manus impression with rectangular and prominent scales.

(C and D) MNG 1765. Forelimb hexagonal scale impressions.

(E–G) MNG 1821. Trunk scale impressions, overview (F), rhomboidal scales (E) and rectangular scales (G).

(H and I) Hindlimb scale impressions. Hexagonal and overlapping (upper left of the photo) and rectangular (lower right of the photo).

(J and K) MNG 14944. Tail scale impressions, rectangular and prominent. All specimens in convex hyporelief; scale bars, 5 cm. 1–9, vertical sections of photogrammetric 3D models of the specimens. Note the asymmetric scale profile in 7 and the strongly concave scale profiles with clear hinge regions in 1, 8, and 9.

right forelimb almost parallel to the body and the manus imprint turned medially. The body impressions do not seem to overlap.

Remarks

We introduce a new ichnotaxon, *Bromackerichnus requiescens* n. igen. n. isp. for the described body impressions (Figure 1). They are unequivocally associated with footprints that we assign to *Dimetropus leisnerianus* because they are ectaxonic, ending with claw traces, with laterally elongated palm/sole impressions and digits more deeply impressed at their base and at their end¹¹ (Figures 1A, 2A, and 2B). This material represents body impressions of tetrapods, based on the morphology and arrangement of the different body parts, including trunk, limb, and tail regions. Also, the regular rows of polygons are identified as scale impressions because their morphology and arrangement are consistent, regular, and repeated and found only on the body impressions (Figures 2, S2, and S3). This differs from structures such as interference ripples (e.g., “*Hauboldichnus*,” see the discussion in Haubold¹²) and from microbially induced sedimentary structures (Figure S4), sometimes mistaken for scale impressions.¹³ For the first time, we propose an ichnotaxonomic assignment of the body impressions from the Tambach Formation (including a detailed description of the body impressions and scales) and demonstrate their anatomical connection with *D. leisnerianus* tracks, all of which were not attempted in previous work.^{12,14} The body impressions described herein differ from other early tetrapod amphibian impressions, such as *Hermundurichnus*,⁹ *Temnocorpicinus*,¹⁰ and other unnamed amphibian^{15,16} and reptile¹⁷ body impressions, because of the

with proximal-lateral elongated sole impression, claw traces, rectangular scales (Figures 2A and 2B; section 1), and sometimes digit drag traces are observed in MNG 1822, 1983, 13490, and 14944. Thin, elongated, and parallel trace sets (Figures 1C and 1D) are visible in several specimens (MNG 1822, 1983, 10058, and 10615).

Aggregation traces

MNG 14944 yields at least four tail impressions (Figures 1C and 1D). The two tail impressions on the left of the slab are directed about 90° compared with each other, and they seem to overlap, which would suggest that the animals left them at a slightly different time. The two tail impressions and partial hindlimbs on the right of the slab are facing opposite directions and do not overlap.

Specimen MNG 1765 (Figure 1B) displays two body impressions aligned side by side (although one is more distal compared with the other) in an almost identical pose. This includes a part of the trunk with visible scalation pattern, a right forelimb with scales, and a manus imprint. Both body impressions show the

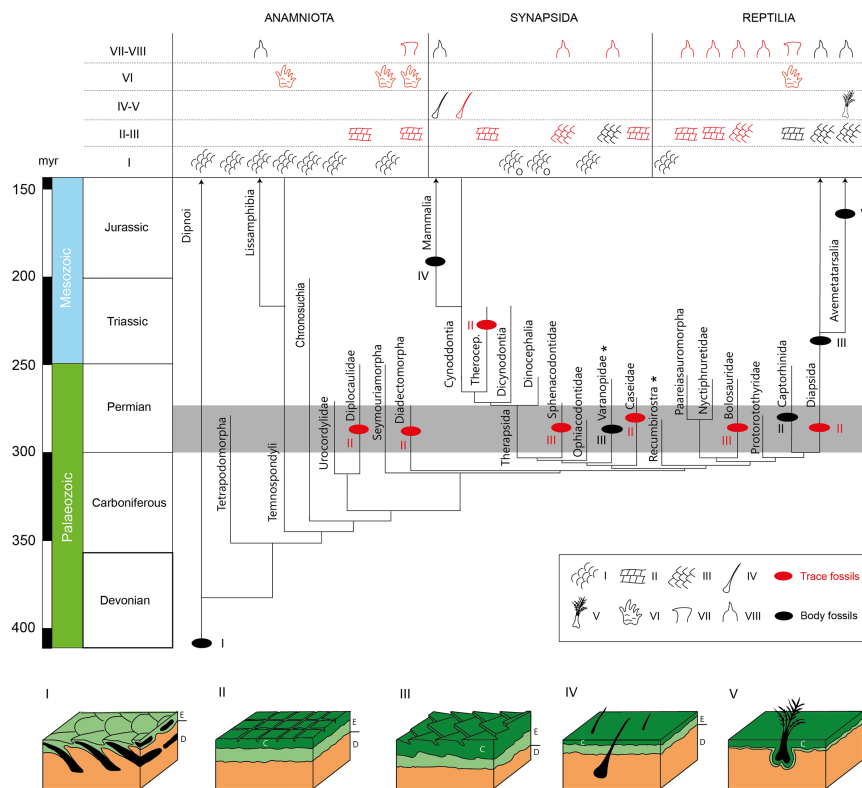


Figure 3. Early evolution of ventral scalation pattern and autopodia skin folds

Cladogram from Mann et al.²⁵ and Ruta et al.²⁶ Asterisks indicate clades with debated phylogenetic position.²² I–VIII, vertebrate integumentary and claw structures; I, dermal scales and other dermal ossifications (o); II, epidermal scales; III, thickened epidermal scales/overlapping scales; IV, hair; V, feathers; VI, skin folds on autopodia; VII, claw sheaths; VIII, claws; D, dermal layer; E, epidermal layer; C, stratum corneum. Ellipses represent the first occurrence of the feature in a specific cladogram branch. Note the high occurrences of new epidermal structures in the early Permian (gray area).

maximal composite length of *Bromackerichnus* n. igen. (about 50 cm, trunk length of MNG 1821 and tail length of MNG 14944, Table S1); nevertheless, some specimens (e.g., MNG 1765) seem smaller.

DISCUSSION

Early tetrapod skin evolution

Epidermal scales (Figures 2, 3, S2, and S3) with a polygonal shape forming

overall morphology of the trunk, limbs, scalation patterns, and associated tracks (Figures 1 and 2).

Tracemakers

Dimetropus leisnerianus tracks have been attributed to pelycosaur-grade synapsids,¹¹ with the exception of varanopids. Few non-varanopid synapsid genera are time-equivalent with the stratigraphic range of the Bromacker site (Figure S1), and even less have a completely known postcranial skeleton and autopodia. At the Bromacker locality, skeletal remains of non-varanopid synapsids have been found, including the spenacodontid *Dimetrodon teutonius* and the caseid *Martensius bromackerensis*.^{18,19} Both show a large tarsus and a digital arcade in the digits (Figure S5), both features consistent with the proximal-lateral elongate sole impression and the paw-like impressions of *Dimetropus leisnerianus*. We compared trace fossil measurements for *Bromackerichnus* n. igen. and the associated *Dimetropus leisnerianus* with skeletal measurements of a selection of potential non-varanopid synapsid producers of the same age of the Bromacker locality (STAR Methods; Tables S1 and S2). Results indicate that *Martensius* has a noteworthy longer manual digit V compared with the *Dimetropus leisnerianus* footprints. *Palaeohatteria* has a gleno-acetabular length too short and *Ophiacodon* shows a pes/manus length ratio too high compared with the trace fossils. Because *Edaphosaurus* and *Sphenacodon* do not occur at the Bromacker locality (and *Ophiacodon* not even in Europe), it is reasonable to assume that *Bromackerichnus* n. igen. and the associated *Dimetropus leisnerianus* were produced by *Dimetrodon teutonius* or similarly proportioned yet unknown synapsids. The calculated maximal snout-vent distance of *D. teutonius* (55 cm, Berman et al.¹⁸) is comparable with the

maximal composite length of *Bromackerichnus* n. igen. (about 50 cm, trunk length of MNG 1821 and tail length of MNG 14944, Table S1); nevertheless, some specimens (e.g., MNG 1765) seem smaller.

rows in a grid-like or alternating arrangement are found only in reptiles⁶ (including birds²⁰) among extant tetrapods. *Bromackerichnus* n. igen. shows rows of prominent polygonal scales with a definite hinge region (Figure 2), this is in agreement with the development of epidermal scales in early synapsids. As such, the earliest occurrences of epidermal scales in synapsids are from the early Permian trace fossil record, and specifically from the Sakmarian of Germany (Tambach Formation, this study) and the Artinskian of France (Rabejac Formation, this study), attributed to spenacodontids and caseids, respectively. This type of integument is also known from early Permian varanopids, from the Sakmarian of Germany (Leukersdorf Formation²¹); however, varanopids are currently considered either synapsids or reptiles.²² Impressions of epidermal scales are visible in Middle Triassic footprints, potentially made by therocephalians.²³ Epidermal scales may therefore have had a long stratigraphic range in non-mammalian synapsids (Cisuralian-Middle Triassic) and potentially occurred in at least three different families. Crown-group mammals appeared in the Late Triassic and may have acquired endothermy (and thus hair) no later than the Jurassic.²⁴ Whether the co-occurrence of scaly skin and hairy appendages was common in early Mesozoic mammal relatives or whether transitional skin structures occurred is not clear from the fossil record.

The first occurrences of epidermal scales in the reptile body fossil record are in the early Permian, specifically captorhinids from the Artinskian of Oklahoma (Richard Spur fissure fills)²⁷ and in the trace fossil record of parareptile and diapsid traces, both from the Asselian of Germany (Goldlauter Formation).^{12,17} The earliest potential record of these structures in anamniotes is in the early Permian trace fossil record, from the Asselian of

Germany (Rotterode Formation) and Poland (Ślupiec Formation), attributed to the groups Nectridea⁹ and Diadectomorpha,²⁸ respectively.

Rows of overlapping epidermal scales (Figures 2, 3, S2, and S3) are characterized by a zigzag-like surface due to the sigmoidal folding of the epidermis. In modern animals, these structures are found only in the highly cornified skin of reptiles.⁶ Among synapsids, a similar structure is observed in spheonacodontid trace fossils from the Sakmarian of Germany (Tambach Formation, this study). In the fossil record of reptiles, morphological indications for overlapping scales are observed in Triassic diapsid skeletons and tracks.²⁹ The earliest occurrence is in an early Permian trace fossil of parareptiles, from the Asselian of Germany (Goldlauter Formation^{11,17}). In the amniote skeletal record, one of the earliest occurrences is in early Permian varanopids, from the Sakmarian of Germany (Leukersdorf Formation²¹).

The overall similarity of epidermal scalation shared by distinct groups of early amniotes is noteworthy, as well as the fact that its earliest fossil occurrence in six different amniote and two anamniote groups (or 7 amniote and 1 anamniote groups, depending on the phylogenetic placement of diadectomorpha³⁰) was in the early Permian (Figure 3). The occurrence of epidermal scales in the last common ancestor of amniotes is supported by trace fossils attributed to amniote stem groups with likely impressions of epidermal skin featuring scalation.^{9,28} Because similar epidermal scales are observed in both modern reptiles and early amniotes, including prominent and overlapping epidermal scales in both early reptiles²⁷ and synapsids (this study), we assume that this similarity is due to a common origin of these skin structures, probably in the Carboniferous. Subsequently, the evolution of epidermal scales in reptiles and synapsids may have followed a similar convergent adaptation. In fact, studies on extant reptilian epidermal scales show that they have different derived mechanisms of cornification.^{31,32} The spreading of epidermal scales to eight different groups and the acquisition of more reinforced epidermal structures in reptiles and synapsids points to an adaptation to dryer paleoenvironments during the early Permian global warming⁸ which required integuments to become more suitable at retaining body water.

Early synapsid group behavior

The combined study of exceptionally preserved trace fossils and depositional environments of the Bromacker locality provides unique information on the paleoecology of spheonacodontids.

Some specimens display multiple resting traces assigned to *Bromackerichnus* n. igen. Such concentration of body impressions of the same producer in a small area would suggest an aggregation behavior. In fact, we interpret the resting traces on MNG 14944 as body impressions of four different individuals (Figure 4B) because they have very different orientation and no transitions between one trace and the other is visible, as it is in documented cases of multiple body traces created by the same individual.¹⁶ Moreover, we interpret the resting traces on MNG 1765 (Figure 4C) as two individuals resting side by side because they do not seem to overlap each other, have a similar orientation, and there is no sign of transition between each other.

The close relation between *Bromackerichnus* n. igen. producers and a muddy, shallow water paleoenvironment is accounted for by the presence of numerous swimming traces

found alongside *Dimetropus* tracks and *Bromackerichnus* n. igen. resting traces (Table S3; Figure 4B). They show the typical morphology and arrangement of swimming traces, with sets of thin, long, and parallel traces.¹¹ Moreover, they differ from drag marks linked to locomotion¹¹ as they do not begin and end with a *Dimetropus* track. In MNG 14944, some of the swimming traces cut the resting traces, suggesting that the resting traces may have been produced underwater. Swimming and sliding traces are preserved in depressed areas in MNG 13490 (Figures 4E and 4F). Moreover, MNG 1823 (Figure 4A) shows parallel trackways of *Dimetropus leisnerianus*, whose preservation changes significantly along their course, suggesting that the animals were moving out of a water pool, consistent with the occurrence of microbial mats and the larger mud crack size, indicating a thicker mud layer.⁵ This evidence would support the hypothesis of possible resting behavior of the *Dimetropus leisnerianus* producers in shallow water (Figure 4G).

The Tambach Formation at the Bromacker locality is characterized by marked wet and dry seasonality.^{5,33} In periods of drought, the spheonacodontid trackmakers of *Bromackerichnus* n. igen. could have gathered in mud ponds. The dorsal sail in early synapsids has been hypothesized to play a thermoregulatory role,³⁴ but although the dorsal sail function is still up for debate,³⁵ mud-bathing could have also helped to keep a cooler temperature. This behavior can be seen in semi-aquatic reptiles nowadays, such as crocodilians in periods of drought.³⁶ Gathering in extant reptiles such as crocodilians can also be for reproductive purposes³⁶ or collaborative hunting.³⁷ Further in agreement with the lifestyle of extant crocodiles, collaborative hunting may primarily have happened at night, as indicated by the supposed nocturnality of spheonacodontids.³⁸ Although the causes are difficult to discern, the described resting traces are strongly suggestive of an early evolution of spheonacodontid aggregation behavior in water pools (Figure 4H).

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to, and will be fulfilled by, the lead contact Dr. Lorenzo Marchetti (lorenzo.marchetti@mfng.berlin).

Materials availability

The authors declare that the specimens MNG, which are the focus of this study, are housed at the Friedenstien Stiftung Gotha, Germany.

Data and code availability

- The studied material is available at publicly accessible institutions. Institutional abbreviations: CM, Canadian Museum of Nature, Ottawa, Ontario, Canada; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MB, Museum für Naturkunde Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNC, Museum für Naturkunde Chemnitz, Germany; MNG, Friedenstien Stiftung Gotha, Germany; NHMW, Naturhistorisches Museum Wien, Austria; MNHN, Muséum National d'Histoire Naturelle, Paris, France; SS, Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie, Freiberg, Saxony, Germany; UGKU, Umweltmuseum Geoskop, Thallichtenberg, Germany; UR, University "La Sapienza" of Rome, Italy.
- All the data used in this study are included in Tables S1–S3.
- All raw computed tomography (CT) scan data and parameters are made available on MorphoSource (MorphoSource ID: 000720516).
- This paper does not report original code.

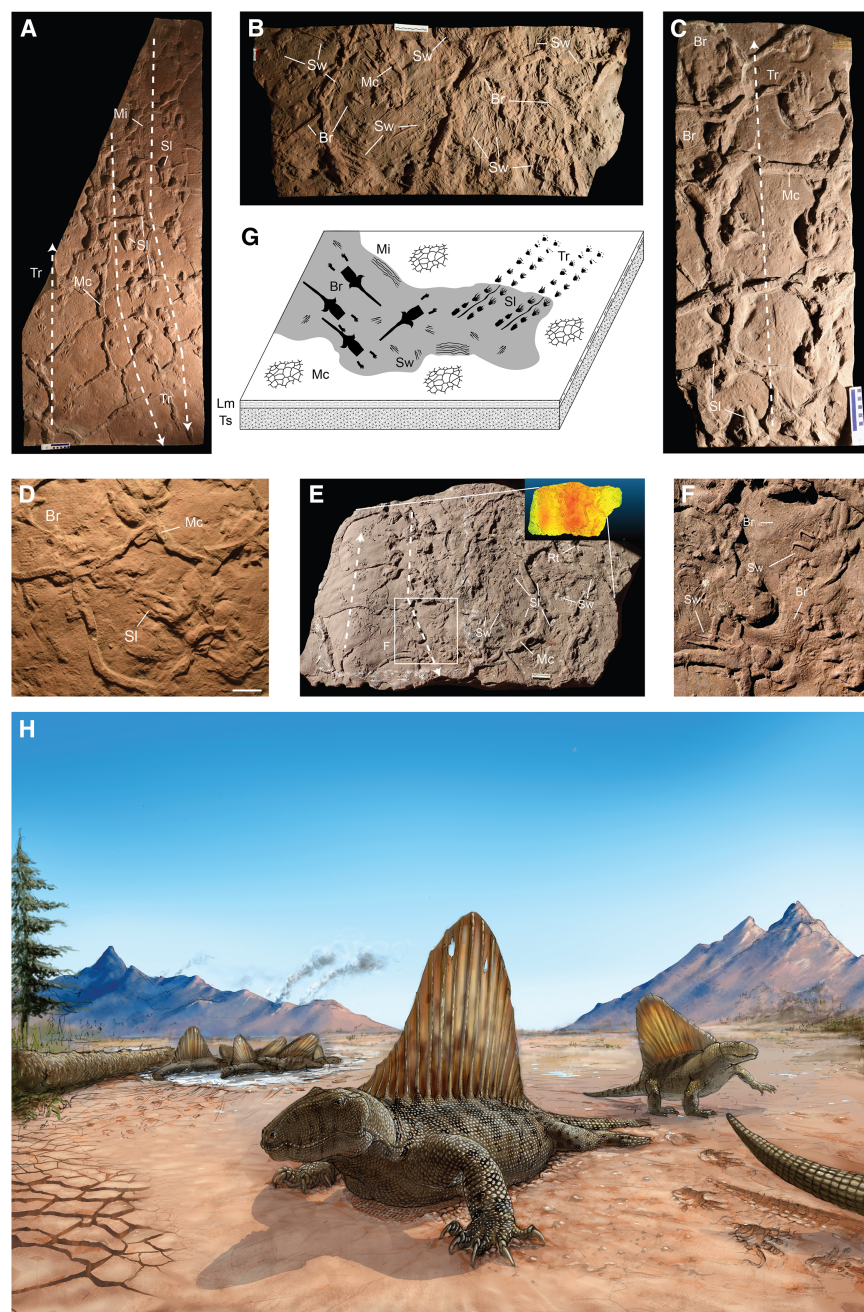


Figure 4. Paleoeology of *Bromackerichnus requiescens* n. igen. n. isp.

(A) MNG 1823. Parallel trackways of *Dimetrodon leisnerianus* changing preservation along their course, associated with microbial mats and cut by mud cracks.

(B) MNG 14944. Four sphenacodontid body impressions of *Bromackerichnus requiescens* n. igen. n. isp., associated with *Dimetrodon leisnerianus* trackways and swimming traces and cut by mud cracks, artificial cast.

(C) MNG 1765. Two *Bromackerichnus requiescens* n. igen. n. isp. laying side to side and a trackway of *Dimetrodon leisnerianus* showing sliding traces, both cut by mud cracks.

(D) MNG 1822. *Bromackerichnus requiescens* n. igen. n. isp. and *Dimetrodon leisnerianus* trackway with sliding traces, cut by mud cracks.

(E and F) MNG 13490. *Bromackerichnus requiescens* n. igen. n. isp. and indeterminate body impressions associated with swimming traces and trackways of *Dimetrodon leisnerianus*, *Ichthyosaurus sphaerodactylus*, and *Varanopus microdactylus*. The trace fossils are cut by mud cracks. Note in the false color depth map from photogrammetric 3D model, in the upper right corner of (E), that the deepest areas in red are those with swimming, sliding, and resting traces.

(G) Paleoenvironmental reconstruction from the combined information of (A)–(E). Note the transition from indistinct footprints with sliding traces to well-preserved footprints in the water-to-land transition, as observed in (A). Br, *Bromackerichnus requiescens* n. igen. n. isp.; Rt, indeterminate resting trace; Sw, sphenacodontid swimming traces; Sl, sliding traces; Tr, sphenacodontid trackways; Mi, microbially induced sedimentary structures (MISS); Mc, mud cracks; Lm, thin laminated mudstone; Ts, tabular fine- to medium-grained sandstone. Arrows indicate the direction of the main trackways. All specimens in convex hyporelief; scale bars, 5 cm.

(H) Group of *Dimetrodon teutonius* resting in a pool. Notice the resting traces, the swimming traces, and the trackways indicating walking out of water. The head scales are hypothetical—they are not present in the studied specimens. Paleoart by Charlene Letenneur.

See also Table S3.

- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

ACKNOWLEDGMENTS

We thank the editor, Florian Maderspacher, and the reviewers, Aaron LeBlanc, Ken Angielczyk, and two anonymous reviewers, for the fruitful discussion. We thank the curator, T. Hübner, and the collection manager, S. König (both MNG), for the assistance during study visits and specimen loans. We thank all curators and collection managers of other institutions with comparative material. We thank C. Letenneur and S. König for the artworks. We thank M. Maier for further preparation, E. Bendel for CT scanning, and S. Seifert and G. Rops for segmenting and exporting 3D models of MNG material. This work has been

funded by the Bundesministerium für Bildung und Forschung (BMBF) for the BROMACKER Project 2020–2025, grant number 01UO2002A.

AUTHOR CONTRIBUTIONS

L.M. ideated the study, studied the material, made measurements, analyzed data, wrote the manuscript, and made figures and tables. A.L. and M.B. studied the material, analyzed data, wrote the manuscript, and made figures. J.F. analyzed data and wrote the manuscript. All authors revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
 - Specimen collection
- METHOD DETAILS
 - Biostratigraphy
 - 3D model generation
 - Taphonomy
 - Systematics
 - Nomenclatural acts
- QUANTIFICATION AND STATISTICAL ANALYSIS
 - Skeletal and trace fossil measurements

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2025.04.077>.

Received: January 26, 2025

Revised: March 24, 2025

Accepted: April 30, 2025

Published: May 23, 2025

REFERENCES

1. Romer, A.S. (1956). *Osteology of the Reptiles* (The University of Chicago Press).
2. Reisz, R. (1975). Pennsylvanian pelycosaurs from Linton, Ohio and Nýřany, Czechoslovakia. *J. Paleontol.* 49, 522–527.
3. Jasinoski, S.C., and Abdala, F. (2017). Aggregations and parental care in the Early Triassic basal cynodonts *Galesaurus planiceps* and *Thrinaxodon liorhinus*. *PeerJ* 5, e2875. <https://doi.org/10.7717/peerj.2875>.
4. Smith, R.M., Angielczyk, K.D., Benoit, J., and Fernandez, V. (2021). Neonate aggregation in the Permian dicynodont *Diictodon* (Therapsida, Anomodontia): evidence for a reproductive function for burrows? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 569, 110311. <https://doi.org/10.1016/j.palaeo.2021.110311>.
5. Eberth, D.A., Berman, D.S., Sumida, S.S., and Hopf, H. (2000). Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach Basin (Thuringia, central Germany): the upland holy grail. *Palaios* 15, 293–313. [https://doi.org/10.1669/0883-1351\(2000\)015<0293:LPTPAV>2.0.CO;2](https://doi.org/10.1669/0883-1351(2000)015<0293:LPTPAV>2.0.CO;2).
6. Sian Rutland, C.S., Cigler, P., and Kubale, V. (2019). Reptilian skin and its special histological structures. In *Veterinary Anatomy and Physiology*, C. Sian Rutland, and V. Kubale, eds. (IntechOpen), pp. 135–156. <https://doi.org/10.5772/intechopen.84212>.
7. Ji, Q., Luo, Z.X., Yuan, C.X., and Tabrum, A.R. (2006). A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science* 311, 1123–1127. <https://doi.org/10.1126/science.1123026>.
8. Marchetti, L., Forte, G., Kustatscher, E., DiMichele, W.A., Lucas, S.G., Roghi, G., Juncal, M.A., Hartkopf-Fröder, C., Krainer, K., Morelli, C., et al. (2022). The Artinskian Warming Event: an Euramerican change in climate and the terrestrial biota during the early Permian. *Earth Sci. Rev.* 226, 103922. <https://doi.org/10.1016/j.earscirev.2022.103922>.
9. Walter, H., and Werneburg, R. (1988). Über Liegespuren (Cubichnia) aquatischer Tetrapoden (? Diplocauliden, Nectridea) aus den Rotteröder Schichten (Rotliegendes, Thüringer Wald/DDR). *Freiberg. Forsch. H.* 419, 96–106.
10. Lucas, S.G., Fillmore, D.L., and Simpson, E.L. (2010). Amphibian body impressions from the Mississippian of Pennsylvania, USA *Ichnos* 17, 172–176. <https://doi.org/10.1080/10420940.2010.502488>.
11. Marchetti, L., Mújal, E., Logghe, A., Buchwitz, M., Klein, H., and Lucas, S. G. (2025). Permian vertebrate tracks. In *Vertebrate Ichnology*, S.G. Lucas, A.P. Hunt, and H. Klein, eds. (Elsevier), pp. 87–178. <https://doi.org/10.1016/B978-0-443-13837-9.00007-X>.
12. Haubold, H. (1972). Panzerabdrücke von Tetrapoden aus dem Rotliegenden (Unterperm) des Thüringer Waldes. *Geologie* 21, 110–115.
13. Niedźwiedzki, G., and Bojanowski, M.A. (2012). A Supposed eupelycosaur body impression from the Early Permian of the Intra-Sudetic Basin, Poland. *Ichnos* 19, 150–155. <https://doi.org/10.1080/10420940.2012.702549>.
14. Pabst, W. (1908). Die Tierfährten in dem Rotliegenden „Deutschlands“. *Nova Acta Leopoldina* 89, 316–481.
15. Langiaux, J. (1980). Premières observations a Morteu (Stéphanien de Blanz-Montceau) ichnites, faune, flore. *Revue Périodique de Vulgarisation des Sciences Naturelles et Historiques “La Physiophile” Montceau-le-Mines* 93, 77–88.
16. Groenewald, D.P., Krüger, A., Day, M.O., Penn-Clarke, C.R., Hancox, P.J., and Rubidge, B.S. (2023). Unique trackway on Permian Karoo shoreline provides evidence of temnospondyl locomotory behaviour. *PLoS One* 18, e0282354. <https://doi.org/10.1371/journal.pone.0282354>.
17. Martens, T. (1991). Ein besonderes Fossil. *Paläontol. Z.* 65, 225–226. <https://doi.org/10.1007/BF02989841>.
18. Berman, D.S., Henrici, A.C., Sumida, S.S., and Martens, T. (2004). New material of *Dimetrodon teutonis* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany. *Ann. Carnegie Mus.* 73, 108–116.
19. Berman, D.S., Maddin, H.C., Henrici, A.C., Sumida, S.S., Scott, D., and Reisz, R.R. (2020). New primitive caseid (Synapsida, Caseasauria) from the early Permian of Germany. *Ann. Carnegie Mus.* 86, 43–75. <https://doi.org/10.2992/007.086.0103>.
20. Stettenheim, P.R. (2000). The integumentary morphology of modern birds—an overview. *Am. Zool.* 40, 461–477.
21. Spindler, F., Werneburg, R., Schneider, J.W., Luthardt, L., Annacker, V., and Rößler, R. (2018). First arboreal ‘pelycosaurs’ (Synapsida: Varanopidae) from the early Permian Chemnitz Fossil Lagerstätte, SE Germany, with a review of varanopid phylogeny. *PalZ* 92, 315–364. <https://doi.org/10.1007/s12542-018-0405-9>.
22. Ford, D.P., and Benson, R.B. (2020). The phylogeny of early amniotes and the affinities of Parareptilia and Varanopidae. *Nat. Ecol. Evol.* 4, 57–65. <https://doi.org/10.1038/s41559-019-1047-3>.
23. Marchetti, L., Collareta, A., Belvedere, M., and Leonardi, G. (2021). Ichnotaxonomy, biostratigraphy and palaeoecology of the Monti Pisani tetrapod ichnoassociation (Tuscany, Italy) and new insights on Middle Triassic Dinosauromorphs. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 567, 110235. <https://doi.org/10.1016/j.palaeo.2021.110235>.
24. Newham, E., Gill, P.G., and Corfe, I.J. (2022). New tools suggest a middle Jurassic origin for mammalian endothermy: advances in state-of-the-art techniques uncover new insights on the evolutionary patterns of mammalian endothermy through time: advances in state-of-the-art techniques uncover new insights on the evolutionary patterns of mammalian endothermy through time. *BioEssays* 44, e2100060. <https://doi.org/10.1002/bies.202100060>.
25. Mann, A., Calthorpe, A.S., and Maddin, H.C. (2021). Joermungandr boliti, an exceptionally preserved ‘microsaur’ from the Mazon Creek Lagerstätte reveals patterns of integumentary evolution in Recumbirostra. *R. Soc. Open Sci.* 8, 210319. <https://doi.org/10.1098/rsos.210319>.
26. Ruta, M., Jeffery, J.E., and Coates, M.I. (2003). A supertree of early tetrapods. *Proc. Biol. Sci.* 270, 2507–2516. <https://doi.org/10.1098/rspb.2003.2524>.
27. Mooney, E.D., Maho, T., Philp, R.P., Bevitt, J.J., and Reisz, R.R. (2024). Paleozoic cave system preserves oldest-known evidence of amniote

- skin. *Curr. Biol.* 34, 417–426.e4. <https://doi.org/10.1016/j.cub.2023.12.008>.
28. Voigt, S., Calábková, G., Ploch, I., Nosek, V., Pawlak, W., Raczynski, P., Spindler, F., and Werneburg, R. (2024). A diadectid skin impression and its implications for the evolutionary origin of epidermal scales. *Biol. Lett.* 20, 20240041. <https://doi.org/10.1098/rsbl.2024.0041>.
29. Lallensack, J.N., Buchwitz, M., and Romilio, A. (2022). Photogrammetry in ichnology: 3D model generation, visualisation, and data extraction. *J. Paleontol. Tech.* 22, 1–18.
30. Ponstein, J., MacDougall, M.J., and Fröbisch, J. (2024). A comprehensive phylogeny and revised taxonomy of Diadectomorpha with a discussion on the origin of tetrapod herbivory. *R. Soc. Open Sci.* 11, 231566. <https://doi.org/10.1098/rsos.231566>.
31. Holthaus, K.B., Eckhart, L., Dalla Valle, L., and Alibardi, L. (2018). Review: Evolution and diversification of corneous beta-proteins, the characteristic epidermal proteins of reptiles and birds. *J. Exp. Zool. B Mol. Dev. Evol.* 330, 438–453. <https://doi.org/10.1002/jez.b.22840>.
32. Alibardi, L. (2016). The process of cornification evolved from the initial keratinization in the epidermis and epidermal derivatives of vertebrates: A new synthesis and the case of sauropsids. *Int. Rev. Cell Mol. Biol.* 327, 263–319. <https://doi.org/10.1016/bs.ircmb.2016.06.005>.
33. Pint, A., Hildebrandt, A., Landwehrs, J., Feulner, G., Scholze, F., Nyakatura, J., Ispas, L., Grützner, C., and Frenzel, P. (2023). Contour marks as potential indicators of evaporation rates in the early Permian continental vertebrate site Bromacker (Thuringia, Central Germany). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 628, 111749. <https://doi.org/10.1016/j.palaeo.2023.111749>.
34. Bennett, S.C. (1996). Aerodynamics and thermoregulatory function of the dorsal sail of *Edaphosaurus*. *Paleobiology* 22, 496–506. <https://doi.org/10.1017/S0094837300016481>.
35. Huttenlocker, A.K., Rega, E., and Sumida, S.S. (2010). Comparative anatomy and osteohistology of hyperelongate neural spines in the sphenodontids *Sphenacodon* and *Dimetrodon* (Amniota: Synapsida). *J. Morphol.* 271, 1407–1421. <https://doi.org/10.1002/jmor.10876>.
36. Smith, E.N. (1979). Behavioral and physiological thermoregulation of crocodilians. *Amer. Zool.* 19, 239–247. <https://doi.org/10.1093/icb/19.1.239>.
37. Dinets, V. (2015). Apparent coordination and collaboration in cooperatively hunting crocodilians. *Ethol. Ecol. Evol.* 27, 244–250. <https://doi.org/10.1080/03949370.2014.915432>.
38. Angielczyk, K.D., and Schmitz, L. (2014). Nocturnality in synapsids pre-dates the origin of mammals by over 100 million years. *Proc. Biol. Sci.* 281, 20141642. <https://doi.org/10.1098/rspb.2014.1642>.
39. Menning, M., Glodny, J., Boy, J., Gast, R., Kowalczyk, G., Martens, T., Röbber, R., Schindler, T., von Seckendorff, V., and Voigt, S. (2022). The Rotliegend in the Stratigraphic Table of Germany 2016 (STG 2016). *Z. Dtsch. Ges. Geowiss* 173, 3–139. <https://doi.org/10.1127/zdgg/2022/0311>.
40. Dhouailly, D. (2009). A new scenario for the evolutionary origin of hair, feather, and avian scales. *J. Anat.* 214, 587–606. <https://doi.org/10.1111/j.1469-7580.2008.01041.x>.
41. Voigt, S. (2005). Die Tetrapodenichnofauna des kontinentalen Oberkarbon und Perm im Thüringer Wald – Ichnotaxonomie, Paläoökologie und Biostratigraphie (Cuvillier).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Trace fossil measurements	This paper	Table S1
Skeletal measurements	This paper	Table S2
Associated traces and sedimentary structures	This paper	Table S3
CT scan data	https://www.morphosource.org/	000720516
Nomenclature acts	https://zoobank.org/	urn:lsid:zoobank.org:act:3A2F6751-9DDB-42E8-812B-52D705F9E83D
Software and algorithms		
Agisoft Metashape Professional	https://www.agisoft.com/	N/A
Cloud Compare	https://www.danielgm.net/cc/	N/A
Paraview	https://www.paraview.org/	N/A
Amira ZIB Edition 2021.09	https://www.thermofisher.com/ie/en/home/electron-microscopy/products/software-em-3d-vis/amira-software.html	N/A
Other		
Holotype specimen of <i>Bromackerichnus requiescens</i> n. igen. n. isp.	This paper	MNG 1821
Paratype specimen of <i>Bromackerichnus requiescens</i> n. igen. n. isp.	This paper	MNG 1765
Paratype specimen of <i>Bromackerichnus requiescens</i> n. igen. n. isp.	This paper	MNG 14944

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Specimen collection

The studied material comes from the early Permian Bromacker locality in Thuringia, central Germany.⁵ This locality, near the village of Tambach-Dietharz, yielded abundant and well-preserved tetrapod footprints and trackways from sandstone quarrying activities since the late 19th century.¹⁴ These trace fossils are usually preserved as convex hyporelief at the base of sandstone layers, the “lower beds” of Eberth et al.⁵ From the 80ies of the 20th century, abundant, well-preserved and articulated tetrapod skeletons have been found from a different lithofacies, fine-grained sandstones and siltstones, the “upper beds” of Eberth et al.⁵ The studied material comes from the “lower beds” of Eberth et al.⁵ and was collected between 1895-1899 in the Seeberger Fahrt quarry (MNG 1765-1987) and after 2000 in the commercial quarry (MNG 13490-14944) of the Bromacker locality.

METHOD DETAILS

Biostratigraphy

All the material from the Bromacker locality (Figure S1) belongs to the Tambach Sandstone Member of the Tambach Formation, lately considered of Sakmarian age, based on biostratigraphy and radiometric ages of the underlying formations.³⁹ The paleoenvironment has been interpreted as an inland fluvial setting in a seasonal tropical climate.⁵

3D model generation

We obtained 3D models of the specimens through digital photogrammetry with the software Agisoft Metashape Professional. Contour lines and colour depth maps were obtained by employing the software Cloud Compare and Paraview. We analyzed the cross-section of scales of different body parts of *Bromackerichnus* n. igen. on 3D models.²⁹

The CT scan was done at the Museum für Naturkunde Berlin, Germany with a YXLON FF35 CT scanner. The segmentation of the CT scans of skeletons was done with the software Amira ZIB Edition 2021.09.

Taphonomy

Preservation of skin is rare in early amniote body fossils and hypotheses about the early evolution of epidermal appendages including scales are commonly based on molecular, morphological, microstructural and developmental studies of extant tetrapods and phylogenetic bracketing.⁴⁰ We analyzed taphonomic processes and modern-day reptile epidermal scales for comparison (Figures S2 and S3), and we found that the late Paleozoic trace fossils that include details of the skin surfaces are somewhat more extensive and span a larger phylogenetic range than the body fossils. So, we argue that it is possible to identify patterns in the evolution of epidermal scales in early amniotes through an integration of the body fossil and trace fossil records of Paleozoic tetrapod skin in a pre-existing phylogenetic framework (Figure 3). The taphonomy of skin impressions has been carefully evaluated, excluding skin-like sedimentary structures such as interference ripples and microbially-induced sedimentary structures (Figure S4). The attribution of skin structures to epidermal scales is based on morphological comparison with modern-day reptile epidermal scales (Figure S2).

Systematics

Body impressions are rarely reported from fossil vertebrates and, if present, are often not considered ichnotaxonically, with few exceptions.^{9,10} We argue that the ichnotaxonomy of such traces is, however, important for paleobiological inferences (Figure S5) and should be based on morphology and consider features that can be related to likely tracemakers. After evaluating the taphonomy of the trace fossils, only the best-preserved and most complete specimens were considered for systematics.¹¹ The proposed ichnotaxonomy is based on a differential diagnosis with morphologically similar resting trace ichnotaxa.

Nomenclatural acts

The nomenclatural acts performed in this work have been registered in ZooBank. The Life Science Identifiers (LSID) for this publication are: urn:lsid:zoobank.org:act:3A2F6751-9DDB-42E8-812B-52D705F9E83D

QUANTIFICATION AND STATISTICAL ANALYSIS

Skeletal and trace fossil measurements

Body impression, footprint and trackway measurements were listed in Table S1, Part of the footprint and trackway measurements are from Voigt⁴¹. Skeletal measurements were listed in Table S2.

Current Biology, Volume 35

Supplemental Information

**Early Permian synapsid impressions
illuminate the origin of epidermal
scales and aggregation behavior**

Lorenzo Marchetti, Antoine Logghe, Michael Buchwitz, and Jörg Fröbisch

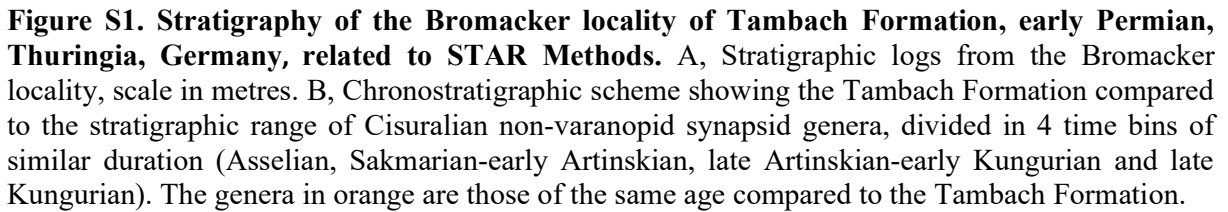


Figure S1. Stratigraphy of the Bromacker locality of Tambach Formation, early Permian, Thuringia, Germany, related to STAR Methods. A, Stratigraphic logs from the Bromacker locality, scale in metres. B, Chronostratigraphic scheme showing the Tambach Formation compared to the stratigraphic range of Cisuralian non-varanopid synapsid genera, divided in 4 time bins of similar duration (Asselian, Sakmarian-early Artinskian, late Artinskian-early Kungurian and late Kungurian). The genera in orange are those of the same age compared to the Tambach Formation.

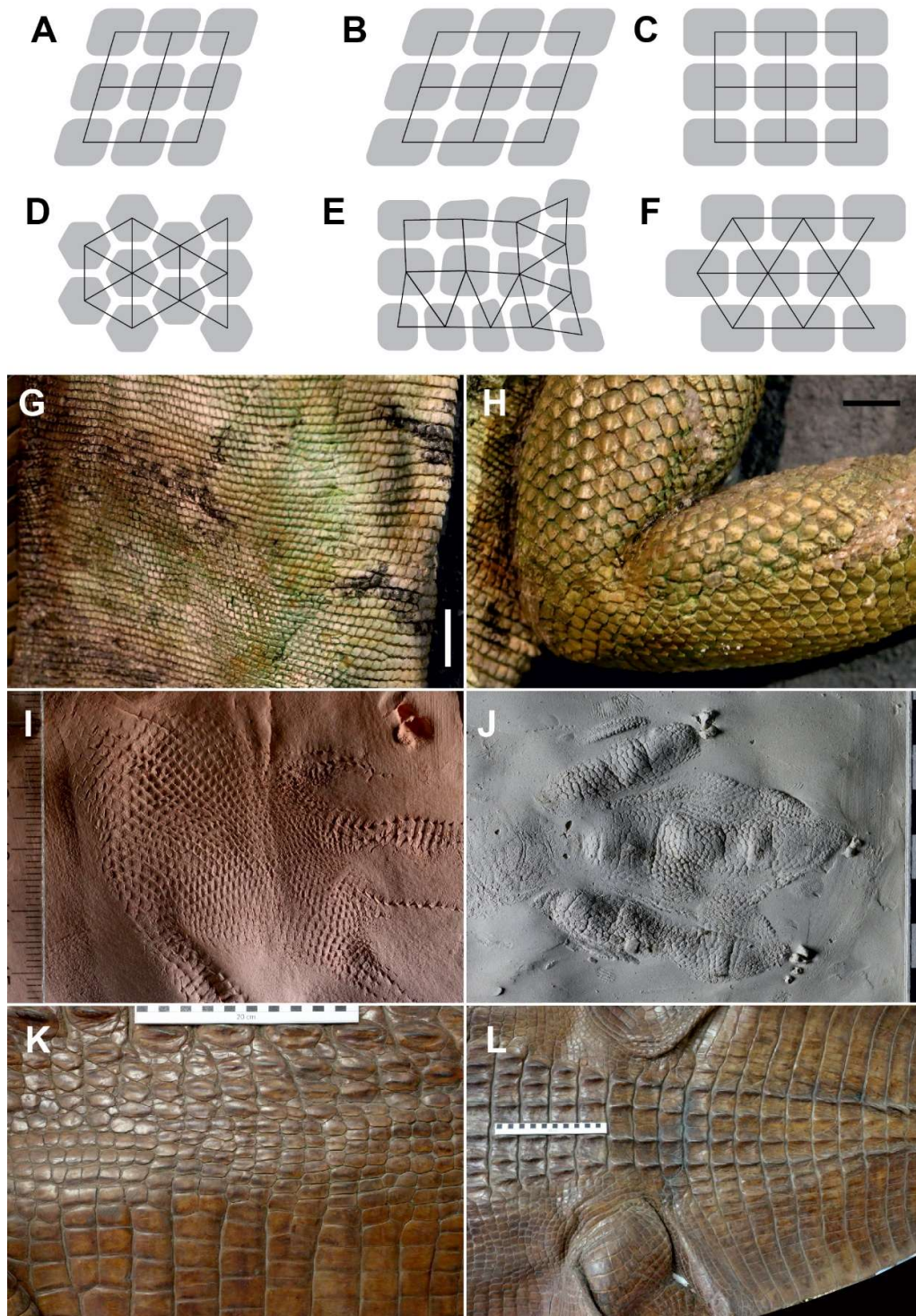


Figure S2. Schematic idealized scalation patterns and their occurrence in extant reptiles, related to STAR Methods. A, Rhombic scales. B, Rhomboid scales. C, Rectangular scales, arranged in an orthogonal grid. D, Hexagonal scales in regular alternating arrangement. E, Polygonal scales in a partly alternating arrangement. F, Rectangular scales, alternating arrangement. G-I, *Iguana iguana*, G, trunk scalation from dorsal (left) to ventral (right). H, Forelimb. I, Pes imprint in clay. J, *Spheniscus demersus*, gypsum cast of a pes imprint. K-L, *Crocodylus porosus*. K, Flattened skin with trunk scalation from dorsal (top) to ventral (bottom). L, Skin of the pelvic region from cranial (left) to caudal (right).

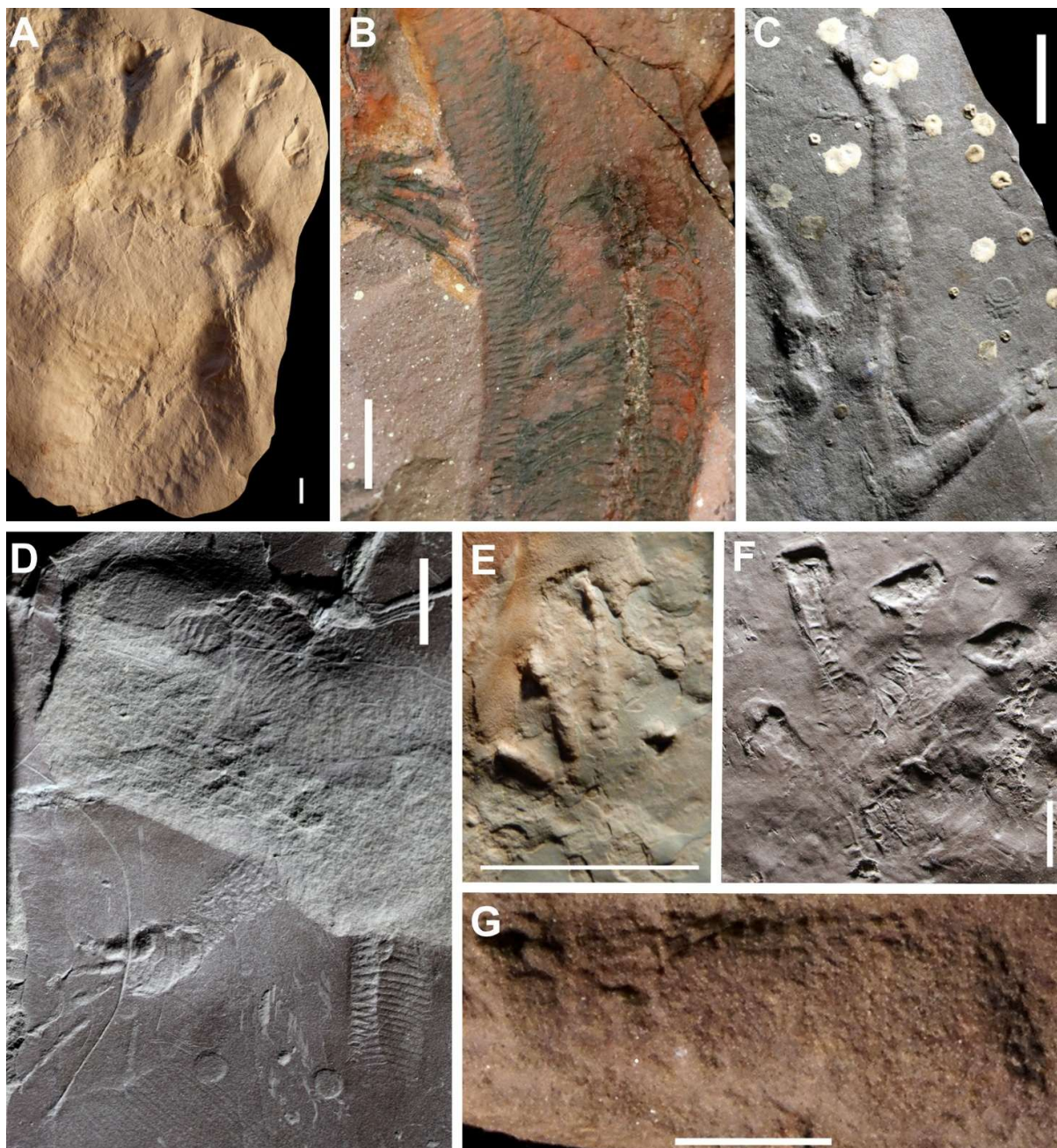


Figure S3. Amniote scalation patterns and skin folds, related to STAR Methods. A, *Dimetropus* isp., MNHN LOD 59, Lodeve Formation, France. Right pes with scales on the sole impression, convex hyporelief, artificial cast. B, *Ascendonanus nestleri*, MNC TA 269, Leukersdorf Formation, Germany. Trunk and right forelimb with scales, ventral view. C, *Dromopus lacertoides*, MNG 7899, Oberhof Formation, Germany. Digit impression with scales, convex hyporelief. D, Body impression with scales on trunk, tail, left hindlimb associated with *Varanopus microdactylus*, MNG 8786, Goldlauter Formation, Germany, concave epirelief. E, *Erpetopus willistoni*, UGKU 1820, Choza Formation, Texas, left pes imprint with scales, convex hyporelief. F, *Hyloidichnus bifurcatus*, UGKU 1965, Peranera Formation, Spain, left manus imprint with skin folds, concave epirelief. G, cf. *Paradoxichnium* isp. UR NS 34-79, Val Gardena Sandstone, Italy, digit imprint with scales, convex hyporelief. Scale bars 1 cm.

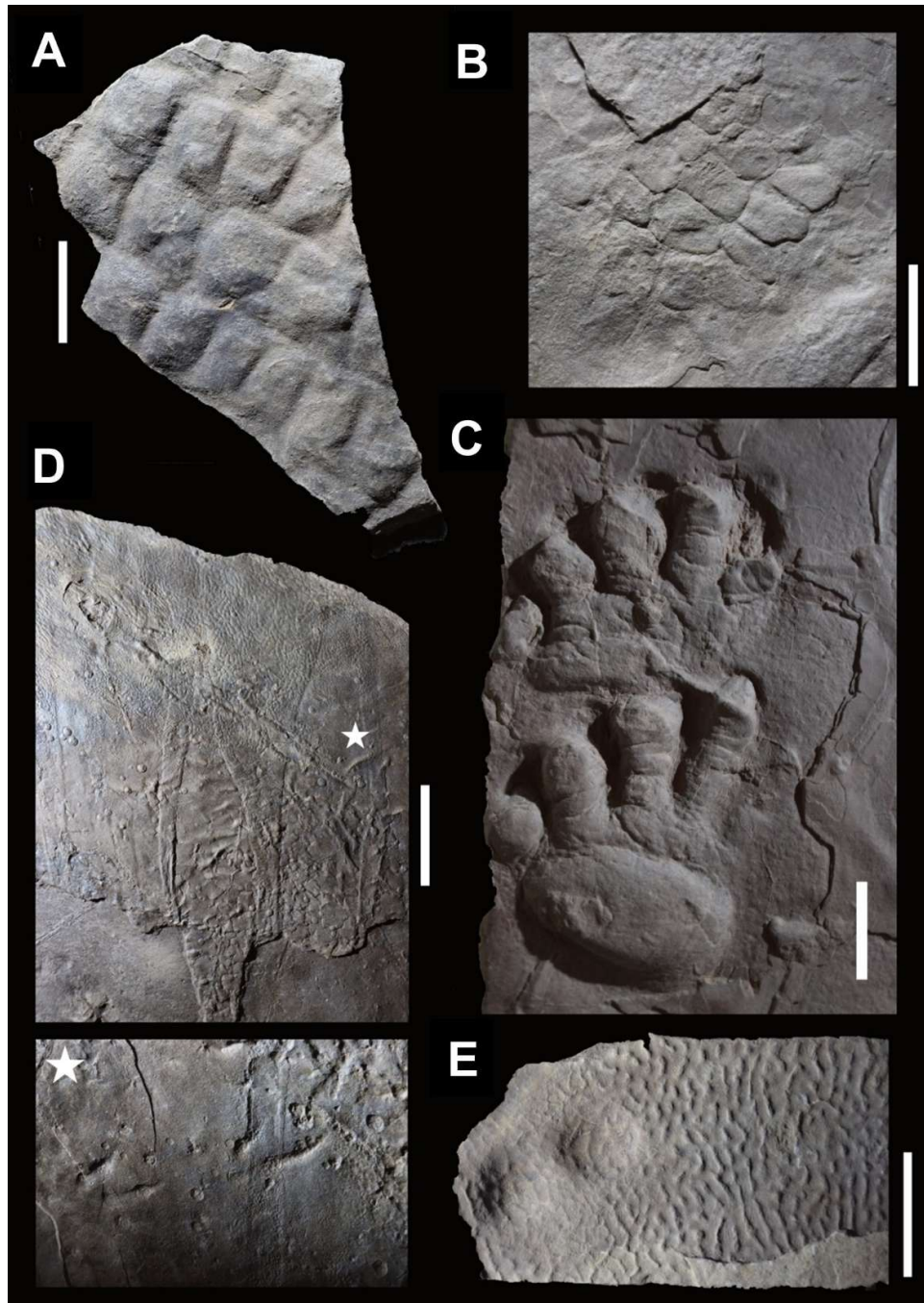


Figure S4. Scale-like sedimentary structures, related to STAR Methods. A, MNG-JF III. Interference ripples. Note the irregular morphology. Scale bar 4 cm. B-E. Microbially-induced sedimentary structures (MISS). B, MNG 2364. “Elephant-skin” reticulate structures. Note the irregular morphology and arrangement. Scale bar 3 cm. C, MB. 1969.54.258. Shallow small bulges on and around *Ichniotherium sphaerodactylum* footprints, convex hyporelief, scale bar 4 cm. D, MNG VF-4277. “Elephant-skin” reticulate structures on and around *Dromopus* isp. footprints, convex hyporelief, scale bar 4 cm. E, MNG-JF 156. Wrinkle structures, scale bar 4 cm.

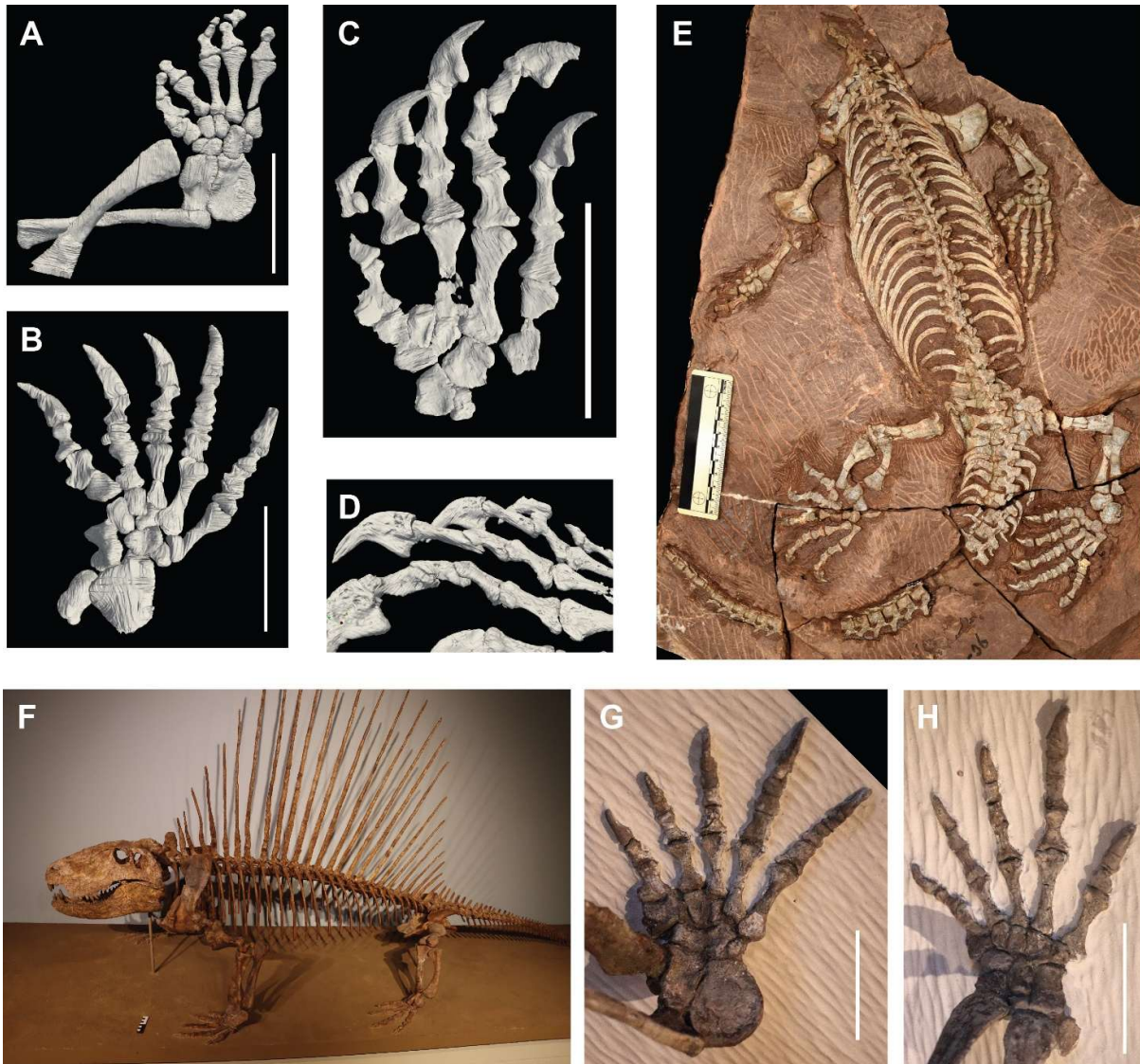


Figure S5. Potential producers of *Bromackerichnus requiescens* n. igen. n. isp., related to STAR Methods. Synapsid taxa from the Bromacker locality, Tambach Formation (A-E) and from other Cisuralian units (F-H). A-D, 3D models from CT scan segmentation. A, *Dimetrodon teutonius*, MNG 10654. Left pes, ventral view. B-E, *Martensius bromackerensis*. B, MNG 13814, left pes, ventral view. C-D, MNG 10595. C, left manus, ventral view. D, left manus, lateral-dorsal view. Note the digital arcade. E, MNG 14230, articulated juvenile skeleton, dorsal view. F, *Dimetrodon grandis*, FMNH UC 764, 775, 781, 796, 1002, 1131 and *D. gigashomogenes*, FMNH UC 112. Composite mounted skeleton, lateral view. G-H, *Dimetrodon milleri*, MCZ 1365. G, Right pes, dorsal view. H, Right manus, dorsal view. Scale bars 5 cm.

Table S1. Trace fossil measurements of *Bromackerichnus requiescens* n. igen. n. isp. and *Dimetropus leisnerianus* from the Bromacker locality, related to STAR Methods. N=specimen number. Measurements on body impressions: IL=impression length, IW=impression width, BL=glenoacetabular length (body length), BW=body width, AL=arm length, AW=arm width, Adiv=arm divarication, LL=leg length, LW=leg width, Ldiv=leg divarication, TL=tail length, TW=tail width. Footprint measurements: FL=footprint length, FW=footprint width, L=digit length, DIV=divarication of digits I-V. Trackway measurements: SL=stride length, PL=pace length, PA=pace angulation, WP=width of pace, D=footprint divarication from midline, Dmp=manus-pes distance, BL=glenoacetabular length (body length). m=manus, p=pes. Digit impressions are indicated by roman numbers. Length measurements in mm, angular measurements in degrees. Footprints and trackway values are averages and partly from ref⁴¹.

Family	Species	N	BL	RW	EW	KW	r/l	FLm	DMLm	MCL	FWm	Lm	ELm	RLm	FLm	VIm	DIVm	r/l	FLp	DMLp	MTL	FWp	ILp	ILp	IIIp	IVp	Vp	DIVp
Casidae	<i>Montemius bromackerensis</i>	MNG 13814	330	152.8			r	112.6	122.6	61.2	83.8	27.7	42.2	46.2	67.2	53.5	43.07	l	123.2	89.9	76.4	104.7	34	38.5	39.3	50	43	65.25
Casidae	<i>Montemius bromackerensis</i>	MNG 10595	251.2	137.9			l	91.4	82.2	55	63.1	23.5	33.3	45.5	46.3	40.9	30.06	r	138.3	104.1	72	75.8	23.9	38.1	56.1	68.5	56.1	28.36
Casidae	<i>Montemius bromackerensis</i>	MNG 14230	272.5	105	168.9	181.7	r	81.6	67.8	35.4	95.1		26.5	39.3	44.6	32.6	48.01	r	93.6	75.6	47	65.5	23.3	31.2	58.5	46.7	37.7	59.28
Edaphosauridae	<i>Edaphosaurus pogonius</i>	FMC	1052.6	275.2	548.6	548.3	l	199.7	162.6	110.8	189.8	48.3	69.9	85	88.9	70	86.86	r	231.8	177.1	134.8	189.1	36.8	58.7	81.5	106.9	85.8	52.44
Edaphosauridae	<i>Edaphosaurus boonerges</i>	MCZ 1366	605.4	290.6	624.6	408.2	r	163	128.4	88.2	117.8	40.9	53.1	68.5	78.4	52.2	50.65	r	172.2	125	100.9	116.8	36.3	56.7	67.4	78.6	57.6	55.55
Ophiacodontidae	<i>Ophiacodon minus</i>	FMC	480.2	155.8	331.2	331.8	r	109.4	90.9	67.7	86.8	15	22.1	31.7	47.5	24.6	91.84	r	158.4	136.8	103.4	135.7	25.9	39.4	48.7	63.6	55.8	71.58
Ophiacodontidae	<i>Ophiacodon minus</i>	FMC	480.2				l	108.7	90.7	72.6	91.7	16.5	23.1	33.5	47.5	27.5	76.59	l	159.5	109.4	87	131.6	21.3	35.5	52.9	68.4	52.3	85.85
Ophiacodontidae	<i>Ophiacodon minus</i>	FMC UC 240					r	116.4	85.7	68.4	87.5	17.2	28	35.6	47.7	27.4	81.1	r	128.1	92.8	84.3	104.1	22.9	37	44.5	46.8	38.3	68.6
Ophiacodontidae	<i>Ophiacodon retroversus</i>	FMC UC 458					l	165.8	116.8	108.3	112.5	26.3	39.5	51.5	68.5	36	65.77	l	224.7	186.2	147.1	177.4	37	54.1	68.8	90.6	65.4	50.44
Ophiacodontidae	<i>Ophiacodon uniformis</i>	MCZ 1366	424.1	214.9	397.6	293.8	r	110.1	78.7	72.3	105.5	11.7	39	37.4	45	24.8	99.82	r	135.8	99.1	86.1	118.5	27	39.4	46.2	64.5	44.4	93.89
Palaeoheterodontidae	<i>Palaeoheterodon longicaudatus</i>	SS 13015-9, 13026-8, 13993	86.1		86	92.4	r	42	36	18.7	27.5	8	12.3	15.2	17	15.4	43.92	l	36.3	34.6	23.5	30	10.7	16.8	19.8	15.8	7.6	45.57
Palaeoheterodontidae	<i>Palaeoheterodon longicaudatus</i>	SS 13531	151.9		122.4	86	r	52.6	48.3	29.3	32.1	10.8	12.2	24	28.6	19.8	43.93	r	85.7	65.3	60	49.4	19.6		26.1	46.4	37.4	28.46
Palaeoheterodontidae	<i>Palaeoheterodon longicaudatus</i>	SS 13630, 13645, 13684	86.1	41.1		88.5																						
Sphenacodontidae	<i>Dimetrodon incisus</i>	FMC UC 1	642.4	430	806.8	564.4	l	210.6	167.9	119.9	147.5	40.9	60.8	81.1	109.7	49	68.74	l	203.2	146.8	111.8	163	36.5	50.4	71.6	93.5	77.8	79.14
Sphenacodontidae	<i>Dimetrodon grandis</i>	FMC	1316.3	365.1	783.2	684.6	r	274.5	199.3	166.2	198.3	32.8	64.2	92.1	123.6	60.6	65.95	r	270.6	207.1	159.8	185.6	43.7	64.5	96.3	112.8	93.1	68.25
Sphenacodontidae	<i>Dimetrodon tetrastis</i>	MNG 10654																l	86.4	95.4	72.7	55						33.69
Sphenacodontidae	<i>Dimetrodon milleri</i>	MCZ 1365	553.3	290.8	464.2	362.4	r	137.2	100.2	82.9	91.4	25.7	37.2	46.6	57.4	29	77.19	r	136.5	92.8	91.7	113.9	26.7	31.7	44.8	57	48.1	78.45
Sphenacodontidae	<i>Sphenacodon ferus</i>	FMC	598.7	211.4	438.9	386.6	r	142.9	107.9	84.3	110.5	20.6	42.1	47.6	67.3	41	68.29	r	144.3	104.4	89.3	123.8	25.2	37.1	44.8	61.6	44.3	82.78
Sphenacodontidae	<i>Sphenacodon ferus</i>	CM 76895																r	99.5	60.7	85.7	88.4						77.63

Table S2. Synapsid skeletal measurements from the Bromacker locality and other sites of similar age, related to STAR Methods. Measurements on skeletons: N=specimen number, BL=glenoacetabular length (body length), RW=ribcage width, EW=width at the elbows, KW=width at the knees, FL=autopodium length, DML=digit-metapodial length, MCL=metacarpal-carpal length, MTL=metatarsal-tarsal length, FW=autopodium width, L=digit length, DIV=divarication of digits I-V, m=manus, p=pes, l=left, r=right. Digit impressions are indicated by roman numbers, length measurements in mm, angular measurements in degrees.

	<i>Bromackerichnus</i>	indet. body impressions	<i>Dimetrodon</i>	<i>Ichthyosaurus</i>	<i>Tambachichnus</i>	<i>Varanopus</i>	swimming traces	drag traces	digging traces	<i>Striatichnus bromackerense</i>	<i>Tambachichnus spiralis</i>	plants	mud cracks
MNG-1765	x		x					x			x		x
MNG-1821	x		x					x			x		x
MNG-1822	x		x					x				X	x
MNG-1828	x		x		x			x			x		x
MNG-1983	x		x					x	x		x		x
MNG-1987	x		x					x		x	x		x
MNG-13490	x	x	x	x		x	x	x			x		x
MNG-14944	x		x				x						x

Table S3. Fossils and sedimentary structures associated with *Bromackerichnus requiescens* n. gen. n. isp., related to Figure 4.